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SEGREGATION OF SUSCEPTIBILITY TO PARASITISM IN MAIZE

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Various degrees of immunity, shown by cultivated plants to the attacks of parasitic organisms, have been recorded. Resistance of cotton, cowpeas, and melons to fungus injury has been reported by Orton (1, 2, 3), of potatoes by Stuart (4), and of flax by Bolley (5). Webber and Orton (6) have shown that the same variety of cowpeas which is resistant to wilt is also markedly resistant to the root knot nematode. Gernert (7) also states that teosinte and first generation teosinte-maize hybrids are not subject to injury by aphids which attack maize.

The inbred strains of maize carried on at the Connecticut Experiment Station, reported by East and Hayes (8), which have been continuously selfed to the present time, show striking differences in the number of plants affected by the smut fungus (*Ustilago zeae* (Beck.) Ung.) and an unidentified leaf blight organism. In 1915 a few inbred strains of flint maize were badly injured by this leaf blight organism. Again in 1916 the same strains were affected in the same way, every plant being badly injured, while other selfed strains derived from different varieties and grown in adjoining rows were almost entirely unaffected. First generation hybrids of these susceptible strains with resistant types were grown in the same field and were only slightly damaged.

In 1917 no injurious effects of this nature could be seen on any plants. Several different strains, however, were badly attacked by smut. In table 1 are given the number of plants grown and the number of plants affected of sixteen different selfed strains of maize, inbred from nine to eleven generations. The relation of these to each other is shown by the pedigree numbers. Twelve of these were derived from one original variety. Of these, three strains were started from single plants in the first generation of inbreeding and numbered 1–6, 1–7, and 1–9. In the third generation from 1–7 two lines were started, 1–7–1–1 and 1–7–1–2, and continued. After the seventh generation all lines were again split up, but at that time the plants were nearing complete homozygosity and the lines which were separated after the

TABLE 1

Susceptibility of Inbred Strains of Maize to Smut (Ustilago zeae)

Pedigree Number	Plot I			Plot II			Plot III		
	Number of Plants Grown	Number of Plants Affected	Percent Affected	Number of Plants Grown	Number of Plants Affected	Percent Affected	Number of Plants Grown	Number of Plants Affected	Percent Affected
10–4–8–3–5–3–4–8–2	29	0	0	227	0	0	—	—	—
10–4–8–3–5–3–4–5–2	21	1	4.76	223	6	2.69	—	—	—
10–3–7–3–9–7–5–1–1	20	0	0	242	3	1.24	113	0	0
10–3–7–3–9–7–5–4–2	25	0	0	274	2	.73	—	—	—
1–9–1–2–4–6–7–5–6–2	31	0	0	183	0	0	84	0	0
1–9–1–2–4–6–7–5–3–2	17	0	0	185	1	.54	96	1	1.04
1–7–1–2–2–9–2–1–1–1–1	27	0	0	86	0	0	—	—	—
1–7–1–2–2–9–2–1–1–4–3	19	1	5.26	196	1	.51	80	0	0
1–7–1–1–1–4–7–5–2–1–1	29	0	0	224	18	8.04	—	—	—
1–7–1–1–1–4–7–5–2–6–1	16	2	12.50	157	15	9.55	—	—	—
1–7–1–1–1–4–7–5–4–7–1	21	3	14.29	211	28	13.27	52	3	5.77
1–7–1–1–1–4–7–5–4–5–2	25	3	12.00	215	21	9.77	—	—	—
1–6–1–3–4–4–4–2–5–5–2	20	0	0	183	0	0	26	0	0
1–6–1–3–4–4–4–2–5–3–2	27	0	0	195	0	0	—	—	—
1–6–1–3–4–4–4–2–4–1–3	30	0	0	211	0	0	—	—	—
1–6–1–3–4–4–4–2–4–4–2	20	0	0	200	0	0	80	0	0

seventh generation remained quite similar. So that for our purpose four distinct lines descending from one original variety and two lines from a different variety can be considered.

These strains were grown in duplicate and some in triplicate plots in three rather widely separated parts of the same field in 1917. Since the same strains show about an equal amount of susceptibility or immunity in all three plots, it seems evident that the pathological

TABLE 2

Summary of Figures Given in Table 1

Pedigree Number	Percent of Plants Affected				Total Number of Plants Grown
	Plot I	Plot II	Plot III	Total	
10–4–etc.	2.00	1.33	—	1.40	500
10–3–etc.	0	.97	0	.74	674
1–9–1–2–etc.	0	.27	.56	.34	596
1–7–1–2–etc.	2.17	.35	0	.49	408
1–7–1–1–etc.	8.79	10.16	5.77	9.79	950
1–6–1–3–etc.	0	0	0	0	992

differences are not due to differences in local infection. Maize was grown on the field the previous year and smut was fairly abundant, so that there was probably as good an opportunity for the plants to become infected in one place as in another. Although smut infection is not considered to come from the seed in the case of maize, the possibility of this factor as a cause of the similar results in the different plots is ruled out because the seed for any one strain grown in the three plots came from different hand-pollinated plants grown the previous year. So that if one strain was badly affected in one plot the fact that it was also affected in another plot was not due to the use of the same contaminated seed. The seed plants of all the different strains were grown in the same place in 1916 and had an equal opportunity of infection.

No data were taken on the infection by smut previous to 1917. It is quite likely that these strains will show variability in the extent to which they are infected by smut in different years, but, as shown in table 1 and summarized in table 2, out of nearly one thousand individuals not a single plant of strain number 1–6–1–3 was affected, while in a nearly equal number of plants of strain number 1–7–1–1 about ten percent of the plants were affected. These two strains were grown in rows side by side in three different plots. The other two strains derived from this same source and the two strains from another variety all show a small amount of infection. Clearly there are marked differences in susceptibility in these strains. The differences are reasonably consistent in the three different places in which the plants were grown and show without a doubt that segregation of susceptibility to

TABLE 3

Susceptibility to Smut of a Non-inbred Variety of Maize, of Two Inbred Strains Derived from this Variety, and of the First and Second Generation Hybrids between These Two Inbred Strains

Pedigree Number	Number of Plants Grown	Number of Plants Affected	Percent of Plants Affected
1	114	2	1.75
1–7–1–1–1–4–7–5–4–7–1	52	3	5.77
1–6–1–3–4–4–4–2–4–4–2	80	0	0
{(1–7–1–1–1–4–7–5–4–7) × (1–6–1–3–4–4–4–2–4–4)} F_1	36	0	0
{(1–7–1–1–1–4–7–5–4–7) × (1–6–1–3–4–4–4–2–4–4)} F_2	97	5	5.15

infection by the smut fungus has taken place during the reduction to homozygosity accompanying the inbreeding process.

Strain number 1–6–1–3, which is not at all affected, is the most vigorous of the four inbred lines derived from variety number 1. It has a darker green color, the plants are larger and more productive than any of the other three. In table 3 the data on smut infection of the first and second generation hybrids of this most resistant strain with the most susceptible strain are given, together with the figures for the two parents and the original non-inbred variety from which the inbred strains were derived. All of these were grown in five adjacent rows in plot III. Owing to the poor germination of the seeds of one of the parents and the first generation of the cross, the numbers are too small to put much reliance upon. Smut was not shown by any plants of the immune parent and of the first generation hybrid, but appeared on some of the plants of the original variety, the susceptible parent, and the second generation of the cross.

The numbers given in table 3 represent all the plants that were grown of the original variety and the second generation hybrid. Of the first generation hybrid, 439 plants in all were grown in different parts of the field. Of these, 2.28 percent were affected, showing that the dominance of immunity is not perfect. When this figure is compared with the 9.79 percent of affected plants of one of the parents, it shows clearly that the hybrid approaches the condition of the immune parent.

As in so many other cases, those factors which enable an organism to attain the best development tend to dominate. The facts given here are considered as additional support to the hypothesis advanced by the writer (9, 10) that the increase in development commonly shown by hybrids is due to the conjunctive action of a large number of favorable, dominant growth factors contributed by both parents.

Resistance is not shown by all first generation hybrids. Biffen (11) finds that some first generation wheat crosses are susceptible to rust and Norton (12) that certain tomato hybrids are susceptible to a wilt disease. On the other hand Vavilov (13) reports wheat hybrids resistant to mildew and Stuckey (14), tomatoes which are resistant to blossom-end rot in the first generations. All these crosses were between types which differed in their susceptibility. Rasmuson (15) with reference to the grape Phylloxera; Van Fleet (16), the chestnut blight; Orton, the melon wilt; Blinn (17), the cantaloupe leaf blight;

Jesse B. Norton (18), the asparagus rust; L. R. Jones (19), the flax wilt; and Gernert with reference to the corn aphis, noted above, all find that resistance tends to be shown in the first generation of crosses between types which are classed as resistant and susceptible.

Although resistance is a highly complex and variable character there can be no doubt but that many types of resistance are determined by definitely inherited factors more or less independent of the environment and of heterosis. There may be certain general principles involved in that certain types of disease thrive best in plants which are in a luxuriant condition either from environmental causes or from the vigor of hybridization. If that were the case resistance would tend to be recessive in those plants which show heterosis markedly. On the other hand certain other infections may be more pronounced in less vigorous plants. In that case heterosis would tend to keep the first generation plants free from the attacks so that the resistance would seem to be dominant.

It is doubtful, however, that in the case of the susceptibility of maize to the smut fungus, reported here, vigor can be more than a minor variating factor. Although the most resistant strain (no. 1–6–1–3) is the most vigorous of the four inbred lines, many naturally crossed varieties are several times as vigorous and productive and are quite susceptible. And there are other inbred strains (nos. 1–9–1–2 and 1–7–1–2) which are no more vigorous than the most susceptible one (no. 1–7–1–1) yet are only slightly susceptible.

The evidence from these inbred strains of maize and their first and second generation hybrids seems conclusive that susceptibility is governed by factors which are capable of being segregated into some lines and not into others and that the modification of the expression of the parasitism by the vigor of the plants is a minor consideration.

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